NOTES ON THE REPRODUCTIVE BIOLOGY OF *ZIGADENUS PANICULATUS*, A TOXIC RANGE PLANT

V. J. Tepedino[1]

ABSTRACT.— *Zigadenus paniculatus* is a toxic plant common on sagebrush foothills at middle elevations in the western United States. Plants produce several racemes from a single stalk. Flowering commences at the base of each raceme and proceeds upwards. The terminal raceme begins blooming first and is followed by lower racemes in sequential order. Flowers are markedly protandrous and incapable of autogamy. Observations do not support the idea that apomixis is a viable reproductive strategy. Plants are mostly self-incompatible; a few seeds were produced from geitonogamous hand pollinations. The pollen/ovule ratio was high, also suggesting outcrossing as the predominant mode of sexual reproduction. A self-incompatibility mechanism may have evolved because the movements of syrphid flies on the inflorescence render protandry alone insufficient to prevent some selfing. The probable presence of toxic substances in the pollen and nectar appears to have reduced the number of potential pollinator species but increased the flower constancy of those species capable of utilizing the floral rewards.

This note describes aspects of the reproductive biology of death camas, *Zigadenus paniculatus* (Nutt.) S. Wats., a toxic range plant that occurs throughout the western United States on plains and foothills usually in association with sagebrush (*Artemisia* spp.). This perennial species commonly produces a single paniculate flowering stalk from a tunicate bulb in spring. Plants probably do not flower until the second or third year (pers. obs.). All plant parts of Z. *paniculatus* and of several other species in the genus contain numerous alkaloids through both vegetative and flowering periods (Willaman and Li 1970). Sheep are particularly susceptible to poisoning because the plant is palatable to them (Stoddart et al. 1949).

Little is known of the reproductive biology of *Zigadenus*, but two of the characteristics considered by Solbrig (1976) to favor outcrossing in plant species, i.e., the perennial habit and occurrence in environments with relatively low climatic predictability, are descriptive of Z. *paniculatus*. In addition, the smallish, creamy white, actinomorphic flowers produce both minute droplets of nectar from glands at the base of each tepal and substantial pollen, and appear adapted for outcrossing by insects. Despite the open structure of the flowers, insect visitation may be restricted to a limited subset of potential pollinators by the presence of toxic substances (probably alkaloids). The pollen, and perhaps nectar, of at least one species (Z. *venenosus* S. Wats.) is toxic to the honey bee (*Apis mellifera* L.) (Hitchcock 1959) and possibly other potential visitors. Baker and Baker (1975) and Rhoades (1979) have hypothesized that the presence of alkaloids in flowers serves to limit visitation to flower-constant visitors and thereby increases the efficiency of the pollination system.

METHODS

A population of about 150 plants on a rocky south-facing slope at Franklin Basin, Logan Canyon, Cache National Forest (altitude 1850 m) in northern Utah was selected for study. Flowering commenced during the first week of June and continued until the end of the month.

For experimental pollination treatments, plants were precaged with chicken wire attached to wooden stakes and wrapped in Saran cloth® (Chicopee Mills, Chicopee, Massachusetts, mesh size 121/cm²) to exclude insect visitors. On each of 25 plants, one flower was used for each of five manipulations: (1) apomicty (flower emasculated before anthers dehisced); (2) autogamy (flowers unmanipulated); (3) geitonogamy (flowers

hand-pollinated with stamens from another flower of the same plant); (4) and (5) xenogamy (flowers hand-pollinated with stamens from a distant plant) with two types of xenogamous pollinations being performed: (4) flowers with style unextended and stigmatic lobes unexposed; (5) flowers with style extended and stigmatic lobes exposed. All non-experimental flowers were removed from the plants, and the position of remaining flowers was noted. The tepals of each experimental flower were also marked with colored dots to facilitate identification. After treatment, all experimental plants were recaged.

Additional plants were collected and returned to the laboratory for examination of the sequence of floral development, and for pollen and ovule counts. The tricarpellate ovaries were dissected under a microscope and the number of ovules in each carpel counted for 10 flowers. The number of pollen grains was estimated by collecting anthers before dehiscence, drying at room temperature for two days, submerging anthers in a known volume of 70 percent alcohol, stirring vigorously with a stirring rod, and then counting grains in subsamples on a haemacytometer.

RESULTS

SEQUENCE OF FLOWER DEVELOPMENT.—The inflorescence of Z. paniculatus is a panicle of 3–7 racemes. Flowering begins at the base of the terminal raceme and proceeds upward. When roughly half of the flowers in the terminal raceme have reached anthesis, flowers at the base of the next highest raceme begin to open. Thus, the sequence of flowering for the entire plant proceeds from the uppermost raceme downward and flowering within a particular raceme proceeds from the base upward.

Individual flowers are protandrous and proceed through several stages. As anthesis begins, the six undehisced swollen anthers emerge through the opening at the top of the flower caused by the parting of the petals. The petals continue to open while the filaments elongate. When the stamens are approximately three times the length of the pistil (including styles), every other anther begins dehiscing. In some cases all anthers

dehisce simultaneously. As dehiscence proceeds, the filaments begin to bend outward away from the female parts that begin extension. Up to this point, the three styles remain bent and lying atop adjacent carpels (hugging position). With dehiscence, the pistil begins to extend and the styles rise off the carpels and proceed toward erection. The spent anthers are then shed and the pistil elongates so that the styles, now bent outward, lie just below the top of the filaments. Thus, male and female phases are discrete and self-pollination within a flower is highly improbable.

POLLEN-OVULE RATIO.— The tricarpellate pistils contained between 23 and 36 ovules ($\bar{x}$ = 29.8 ± 3.98, N = 13), or about 10 ovules per carpel (range 6–12). Production of pollen grains by the six anthers was high ($\bar{x}$ = 391,666 ± 98,456, N = 10) as was the pollen-ovule ratio (13,143 grains per ovule). The high pollen-ovule ratio is another indication that the species is primarily outcrossed (Cruden 1977).

EXPERIMENTAL TREATMENTS.— Unfortunately, after all plants were tagged and experimental pollinations performed, sheep invaded the study site and trampled most plants, both caged and uncaged. Seven of the 25 caged plants were spared and data is presented for these plants only.

Flowers were neither apomictic nor autogamous; none of the seven flowers from each of these treatments produced seeds. Four of seven flowers from the geitonogamy treatments produced a total of six seeds, indicating that plants were mostly self-incompatible but not completely so.

All mature flowers that were cross-pollinated produced seed ($\bar{x}$ = 14.9 ± 6.8) and five of seven cross-pollinated before the styles were fully developed also produced some seed ($\bar{x}$ = 4.1 ± 4.7). Significantly more seed was produced by mature flowers, however (Wilcoxon Signed Rank Test, P = 0.05).

INSECT VISITORS.— Insect visitation to the flowers could only be recorded incidentally, but the agreement between these observations and other published studies is good. The most common visitors to Zigadenus in this and other studies were large, hairy syrphid flies, Eristalis hirtus Loew., and the solitary andrenid bee, Andrena astragali Viereck and

Cockerell, which seems to be a *Zigadenus* specialist (Moldenke and Neff 1974, Moldenke 1976, Hurd 1979, pers. obs.). Examination of pollen grains from the scopae of four female *A. astragali* captured on *Z. venenosus* in southeastern Wyoming in connection with another study revealed only *Zigadenus* pollen (Tepedino, unpublished). Stratiomyid flies (*Stratiomys barbata* Loew, *S. nevadae* Bigot) were also recorded occasionally. Flies were always covered with *Zigadenus* pollen. Beedlow (1979) recorded only muscid flies visiting *Z. elegans* Pursh.

DISCUSSION

Death camas possesses several characteristics that favor outcrossing as the predominant mode of sexual reproduction. Plants are primarily self-incompatible; only half the flowers that were hand-pollinated with anthers from another flower on the same plant set any seed (1–2 per flower). In addition, self-fertilization within an individual flower is most unlikely because the flowers are strongly protandrous; no flowers set seed autogamously. Low levels of autogamy were also found by Beedlow (1979) for *Z. elegans*, a late summer blooming species; only 11 of 143 bagged flowers set any seed. In contrast, Moldenke (1976) described *Zigadenus* (no species given but probably *fremontii* S. Wats.) as moderately self-compatible, but he gave no details.

Zigadenus paniculatus exhibits a pattern of flowering that may be common for plants with vertical inflorescences. Within each of the several racemes, flowering begins at the bottom and proceeds upwards. Coupled with the protandrous habit, this means that in a fully developed raceme, flowers at the bottom are functional females and those at the top are functional males. For some other plant species with single racemes and a similar sequence of floral development, bumble bee pollinators typically land at the bottom of the inflorescence and move upward, thus increasing the probability of cross-pollination and minimizing selfing (Pyke 1978 and references therein). In these species protandry is a sufficient mechanism for the avoidance of selfing and they are, in fact, self-compatible (Pyke 1978).

In *Z. paniculatus* the protandrous habit is not sufficient to avoid self-pollination because of the foraging behavior of flower-visiting flies. Syrphids and stratiomyids were commonly seen to move both between racemes on the same plant and either upward or downward within any given raceme. *Andrena astragali* was easily disturbed by observation, and movements could not be recorded with surety. Thus, if *Z. paniculatus* plants were self-compatible, as were those species studied by Pyke (1978), then much of the seed production would be due to self-pollination as effected by flies. It would seem then that incompatibility mechanisms have evolved subsequent to protandry to insure cross-pollination (Faegri and Van der Pijl 1971).

This preliminary evidence agrees with certain of the predictions of Baker and Baker (1975) and Rhoades (1979) regarding the possible function of alkaloids in floral resources. As predicted, the pollinator fauna visiting *Zigadenus* appears to be a small subset of species that are capable of foraging on the blossoms. Plant species with open blossoms typically have many more insect visitors than have been recorded for *Zigadenus*. The few common visitors to the flowers may also be highly flower constant. As mentioned above, *A. astragali* probably specializes on the collection of pollen and nectar from *Zigadenus* flowers. Syrphid flies are generally thought to be relatively inconstant in their foraging behavior (Faegri and Van der Pijl 1971), but a recent study has shown that a species of *Eristalis* can exhibit strong preferences (Kay 1978). Thus, the toxic components in *Zigadenus* pollen and nectar may indeed encourage flower constancy by pollinators (Rhoades 1979).

LITERATURE CITED

BAKER, H. G., AND I. BAKER. 1975. Studies on nectar-constitution and pollinator-plant coevolution. Pages 100–140 in L. E. Gilbert and P. H. Raven, eds., Coevolution of animals and plants. Univ. of Texas Press, Austin.

BEEDLOW, P. A., III. 1979. Pollination dynamics in two subalpine flower meadows. Unpublished dissertation. Utah State Univ., Logan, Utah. 179 pp.

CRUDEN, R. W. 1977. Pollen-ovule ratios: a conservative indicator of breeding systems in flowering plants. Evolution 31:32–46.

FAEGRI, K., AND L. VAN DER PIJL. 1971. The principles of pollination ecology. 2d rev. ed. Pergamon Press, London.

HITCHCOCK, J. D. 1959. Poisoning of honey bees by death camas blossoms. Am. Bee J. 99:418–419.

HURD, P. D., JR. 1979. Superfamily Apoidea. Pages 1741–2209 in K. V. Krombein, P. D. Hurd, Jr., D. R. Smith, and B. D. Burks, ed., Catalog of Hymenoptera in America north of Mexico, Vol. 2 Apocrita (Aculeata). Smithsonian Institution Press, Washington, D.C.

KAY, Q. O. N. 1978. The role of preferential and assortative pollination in the maintenance of flower colour polymorphisms. Pages 175–179 in A. J. Richards, ed., The pollination of flowers by insects.

Linnean Society Symposium Series No. 6. Academic Press, New York.

MOLDENKE, A. R. 1976. California pollination ecology and vegetation types. Phytologia 34:305–361.

MOLDENKE, A. R., AND J. L. NEFF. 1974. The bees of California: a catalogue with special relevance to pollinator and ecological research. International Biological Program Origin and Structure of Ecosystems Technical Report #74-4. Univ. of California, Santa Cruz.

PYKE, G. H. 1978. Optimal foraging in bumblebees and coevolution with their plants. Oecologia 36:281–293.

RHOADES, D. F. 1979. Evolution of plant chemical defense against herbivores. Pages 3–54 in G. A. Rosenthal and D. H. Janzen, eds., Herbivores: their interaction with secondary plant metabolites. Academic Press, New York.

SOLBRIG, O. T. 1976. On the relative advantages of cross- and self-fertilization. Ann. Mo. Bot. Gard. 63:262–276.

STODDART, L. A., A. H. HOLMGREN, AND C. W. COOK. 1949. Important poisonous plants of Utah. Special Report No. 2, Utah State Agricultural Experiment Station, Logan, Utah.

WILLAMAN, J. J., AND H. L. LI. 1970. Alkaloid-bearing plants and their contained alkaloids. Lloydia (supplement) 33 (3A). 286 pp.